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# Ecological Feedbacks in the Earth System

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**Key Points:**

- The role of our planet's diverse ecological feedbacks in Earth system processes is a major knowledge gap
- We review current knowledge on ecological feedbacks within ecosystems, and between ecological, physical, and biogeochemical processes
- Research priorities involve integrating ecological feedbacks in models, mapping feedbacks across scales, and refining projections for policy

**Supporting Information:**

Supporting Information may be found in the online version of this article.

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**Abstract** Ecological feedbacks are fundamental features of the Earth system, affecting physical processes and chemical cycles. Our understanding of the interactions underlying these feedbacks at different spatial and temporal scales and the extent to which feedbacks affect Earth system functioning remains limited. Climate change and other anthropogenic pressures are already negatively affecting ecological processes in marine, freshwater, and terrestrial ecosystems. These will most likely be amplified in the coming decades under our current warming and socioeconomic pathways. The knock-on impacts on ecological feedbacks have the potential to cause rapid perturbations to the Earth system, and may significantly impact the structure and functioning of ecosystems. Yet, the role of our planet's diverse ecological feedbacks in Earth system processes and the impacts of perturbations are major knowledge gaps. Here we review and synthesize current understanding of ecological feedbacks and how they affect physical and chemical processes. We then consider the implications of ecological feedbacks for analyses of anthropogenically-driven change, development of scientific understanding and models, and provision of scientific advice for policymakers. Finally, we identify three priority future research areas for the rapid assessment and integration of ecological feedbacks in Earth system science: (a) including ecological feedbacks in assessments of global change and Earth system models, (b) incorporating ecological feedbacks across scales, and (c) producing projections suitable for policy advice. Overall, this review presents an urgent call to the scientific community for the rapid development of understanding of ecological feedbacks and integrated ecosystem—Earth system research.

**Plain Language Summary** Organisms in the ocean, lakes, rivers, and on land, interact together, affecting each other and modifying their physical and chemical environments. These ecological interactions form feedback loops, where a change in one part of an ecosystem has knock-on effects that lead to further changes that enhance or reduce the change. Whilst we know these ecological feedbacks are important, we have limited understanding of how they work within and between ecosystems and over larger scales across the world. Ecological feedbacks are also likely to be disrupted due to ongoing climate change and destructive human activities (e.g., deforestation, pollution). Major gaps in our understanding of ecological feedbacks make it difficult to predict how ecosystems are affected by change and the larger scale impacts. Here, we explore what is currently known about ecological feedbacks, how they affect the physical environment and chemical processes, how they may be affected by human-driven environmental changes, and what this means for advising policy makers. We also highlight three priority areas of future research, and the need for rapid development of understanding of ecological feedbacks and their role in globally important processes.

## 1. Introduction

Life is maintained in ecosystems through interactions between living organisms and their environments. The Earth system, which includes the Earth's suite of interlinked biological, chemical, physical, and human processes (Bonan & Doney, 2018; Steffen et al., 2020), involves a complex network of ecological interactions. Changes in

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these interactions can extend throughout and across ecosystems, generating ecological feedbacks, with further consequences for ecosystem structure and functioning (Pausas & Bond, 2022; van Breugel et al., 2024). Such feedbacks occur through connected cycles of processes, where one ecological change produces another change in an ecosystem and/or physical or chemical environment, which in-turn affects the original or further ecological processes (Lafuite & Loreau, 2017; Maxwell et al., 2017; Pausas & Bond, 2022; van Breugel et al., 2024; Wu et al., 2021). Perturbations of ecosystems, whether from human activities or climate change, can disrupt existing feedbacks as well as create new ones. These changes can cascade across scales, altering ecosystem responses and undermining stability—the ability to maintain structure and function (Scheffer et al., 2001). When feedbacks are strongly altered, ecosystems may lose resilience, reducing their capacity to both resist and/or recover from disturbances, potentially triggering rapid shifts if tipping points are exceeded (Armstrong McKay et al., 2022; Chaparro-Pedraza, 2021; Gonzalez et al., 2020; Pichon et al., 2024). Within Earth system analyses and modeling however, there has been little integration of the influence of ecological interactions and the potential for these to generate ecological feedbacks (Arnscheidt & Rothman, 2022; Bonan & Doney, 2018; Lade et al., 2019; Sanders-DeMott et al., 2016).

The future well-being of humanity and the sustainable development of human societies requires healthy and resilient ecological systems within the Earth system (Gupta et al., 2023; Henderson & Loreau, 2018; Raworth, 2017; Rockström et al., 2023; Steffen et al., 2020), which necessitates the provision of appropriate scientific advice for policy development. Although there have been major developments in the understanding of current or future consequences of rapid global ecological changes for the Earth system, many aspects are poorly understood (Kyker-Snowman et al., 2022; Liang et al., 2022; Pörtner et al., 2021). Feedback processes have recently been highlighted as potentially important, but underexplored, risks to societies and economies associated with climate change (Rising et al., 2022). Without the appropriate inclusion of feedbacks, Earth system models (ESMs) may miss important pathways of change and thus generate misleading results of future impacts, leading to potentially inappropriate policy advice and societal responses (Kyker-Snowman et al., 2022; Moore, 2022; O'Connor et al., 2021; Rising et al., 2022). We are gaining an improved understanding of some of the processes involved (Betts, 2006; Green et al., 2017; Pichon et al., 2024; Zeng et al., 2017). However, with rapid changes being observed in ecosystems across the world, there is a critical need to gain a more holistic understanding of ecological feedbacks in ecosystems and improve their representation in ESMs (Bonan & Doney, 2018; IPCC, 2022; Moore, 2022; Wang, Foster, et al., 2023).

Here, we review current understanding and synthesize available information on the importance of ecological feedbacks, their operation across spatial and temporal scales, and their influence on Earth system functioning. We highlight the implications of these feedbacks for understanding the impacts of environmental change within science and policy development, drawing on example case studies. We identify key knowledge gaps and propose a scale-based framework for the vital development of our understanding of ecological feedbacks and their integration in future model development. Our overall assessment urges the scientific community to rapidly advance understanding of ecological feedbacks.

## 2. Current Understanding of the Role of Ecological Feedbacks

Ecological feedbacks result from coupled interactions among organisms or between organisms and their environment (Maxwell et al., 2017; Miller & Allesina, 2023; Pausas & Bond, 2022; van Breugel et al., 2024). These interactions form feedback cycles that may reinforce or amplify perturbations (positive feedback) or dampen and reduce perturbations (negative feedback). Within ecological networks, multiple positive and negative feedbacks can operate simultaneously, collectively shaping ecosystem structure, functioning, and responses to change (O'Connor et al., 2021; Pausas & Bond, 2022; van Breugel et al., 2024). The balance of these feedbacks is central to ecosystem stability, shaping both resilience—the capacity to recover from disturbance—and resistance—the capacity to withstand change without shifting to an alternative state (Holling, 1973; Scheffer et al., 2001).

The ecological communities present across ecosystems today have emerged from the evolutionary successes and persistence via natural selection of species and their interactions under past and current environmental conditions, including natural and human disturbances, which have operated across a wide range of spatial and temporal scales (Payne et al., 2020; Pease, 2024; Sole et al., 2002; Ware et al., 2019). Ecological feedbacks are therefore the result of ecological interactions that have evolved over millennia, and can change on glacial and interglacial timescales (Bender, 2003; Pausas & Bond, 2022).

Studies over the last two decades have shown that ecological interactions with physical and biogeochemical processes are key components of many feedbacks within the Earth system (Figure 1 and Table S1 in Supporting Information S1; Armstrong McKay et al., 2021; Chapin et al., 2008; Subin et al., 2011), and may dampen or amplify climate processes (Lim et al., 2019; Pörtner et al., 2023; Pugnaire et al., 2019; Tian et al., 2019). For example, changing patterns of vegetation cover due to grazing can lead to increases or decreases in albedo, evapotranspiration, biome flammability, and soil carbon storage, which in turn affect water cycles, regional weather patterns, and global carbon budgets, resulting in further ecological change (Avissar et al., 2002; Cheng et al., 2021; Coe et al., 2013; Flores & Staal, 2022; Li et al., 2022). The role of feedbacks involving specific ecological processes (such as how microorganisms influence soil organic carbon feedbacks; Table S1 in Supporting Information S1; Tao et al., 2023), has been highlighted in diverse studies encompassing analyses of biodiversity loss, climate processes (particularly the carbon cycle), climate change, and socio-ecological interactions (e.g., Butt et al., 2023; Henderson & Loreau, 2018; Hotaling et al., 2021; Lade et al., 2019; Pörtner et al., 2023; Figure 1). The role of ecological feedbacks in major climate tipping points has also been emphasized (Armstrong McKay et al., 2022), such as the dieback of the tropical and boreal forests that could lead to further loss of forest and, as with human-induced deforestation, affect biophysical processes (e.g., changing albedo and evapotranspiration; Yu et al., 2015). However, evidence of the importance of ecological feedbacks over larger (spatial and temporal) scales and in influencing tipping points in the wider Earth system is limited (Agrawal et al., 2007; Brook et al., 2013; Lenton et al., 2023). The biosphere is not a single ecosystem but is instead made up of multiple connected ecosystems across the planet, which has meant that ecological feedbacks have been beyond the scope of many previous Earth system analyses.

ESMs simulate the suite of interlinked biological, chemical, physical, and human processes that underlie climate, with the aim of simulating the complex interactions occurring within and between the Earth's atmosphere—land—ocean—sea ice systems (Bonan & Doney, 2018; Fisher et al., 2014; Friedlingstein, 2015; Friedlingstein et al., 2006; Walker & Palevsky, 2025). These models offer the opportunity to provide key insights into how a healthy biosphere can be maintained and sustained such that the services required by humans (e.g., provision of food, water, and energy) will continue to be provided (Bonan & Doney, 2018; IPBES, 2019; IPCC, 2022). The complexity of natural ecosystems (Griffith, 2020; Levin, 1998), combined with a lack of a theoretical framework to represent ecosystems across spatial and temporal scales and computational limitations, has reduced ecological realism in current ESMs, with consequences for climate feedbacks (Kyker-Snowman et al., 2022; Moore, 2022; O'Connor et al., 2021; Pichon et al., 2024). Even with advances in computational capacity, lack of data has often led to insufficient understanding of important ecological feedbacks and has impeded further development of ecology in large-scale models (Bonan & Doney, 2018; Fulton et al., 2019; Geary et al., 2020; Kyker-Snowman et al., 2022; Moore, 2022).

Some aspects of ecological feedbacks, however, are included in current ESMs (Appendix A). For example, the crucial role of biological systems in determining atmospheric $CO_2$ concentration, and hence future climate, has led to major advances in the representation of biogeochemical cycles in ESMs over the last two decades (Bonan & Doney, 2018; Friedlingstein, 2015; Friedlingstein et al., 2006). Models of terrestrial carbon cycles now represent storage and interactions between vegetation, soil carbon pools, and land-cover change (Bonan et al., 2024; Fisher et al., 2014; Sharma et al., 2022). In the marine realm, ocean biogeochemical models simulate aspects of competition in nutrient availability between phytoplankton groups and the impacts of grazing on phytoplankton by zooplankton (Bonan & Doney, 2018; Hense et al., 2017; Walker & Palevsky, 2025). The elucidation of the role of ecological feedbacks in global carbon budgets, demonstrates their importance in the Earth system and in the evolution of anthropogenically-driven climate change (Armstrong McKay et al., 2021; Lowe & Bernie, 2018). Consequently, the lack of appropriate representation of climate-ecosystem feedbacks in current models may limit the validity of future predictions of ecosystem responses under climate change scenarios. Yet, apart from specific examples, the role of such ecological feedbacks within the Earth system is largely unexplored in ESMs (Armstrong McKay et al., 2021; Bonan & Doney, 2018; Donges et al., 2021; Pausas & Bond, 2022), and may be particularly important in determining responses to change over the next few years to decades. These are timescales over which ecological processes are crucial and central to many of the key issues policymakers will face in the coming years. Without an appropriate level of representation of ecosystem processes and feedbacks, projections of the future state of the Earth system over the coming decades may indicate incorrect future outcomes and policy recommendations (Bonan & Doney, 2018; Donges et al., 2021; Rising et al., 2022).


**Figure 1.** Examples of feedbacks involving interactions between ecological, biogeochemical, and physical processes at different scales in the Earth system. The text circles around the globe give examples of ecological, biogeochemical, and physical processes involved in ecological feedback cycles (BVOCs = Biogenic volatile organic compounds). The illustrations surrounding the globe provide examples of ecological feedback cycles. Examples of the spatial operation of each of these ecological feedback examples are highlighted by the white arrows on the globe. Links between feedback cycles demonstrate the connectedness of ecological feedback cycles within the Earth system (e.g., seasonal mass migration of birds (1) may involve migration into habitats where vegetation-fire feedback cycles (2) are also important). Examples: 1. *Bird migrations generate feedbacks between ecosystems.* Each year, birds migrate across the globe, connecting remote terrestrial, freshwater, and marine ecosystems, and resulting in transfers of energy, biomass, carbon, and nutrients, and the migrations generate feedbacks between systems (e.g., Bauer & Hoye, 2014; Hahn et al., 2008; Michelutti et al., 2009; Sanchez-Zapata et al., 2007; Zacheis et al., 2001). For example, nutrient transfers can enhance productivity in an overwintering region, increasing food availability and hence survival of the migrating species, leading to population increases in summer breeding habitats. 2. *Fire and resulting vegetation-ecosystem processes generate feedbacks affecting ecosystem structure and function.* The frequency of fires affects vegetation characteristics, which impacts soil structure and carbon storage, hydrographic and biogeochemical cycles and in-turn affects biodiversity, community structure and resilience to fire (e.g., Archibald et al., 2018; Harris et al., 2016; McLauchlan et al., 2020; Staver et al., 2011a; Thapa et al., 2022). 3. *Marine mammals affect ocean-nutrient and carbon budgets generate upper ocean productivity feedbacks.* Whales consume plankton and recycle nutrients in the upper ocean affecting phytoplankton productivity and carbon export to the deeper ocean, and many undertake large seasonal migrations transferring nutrients, affecting productivity in remote ecosystems (e.g., Bauer & Hoye, 2014; Doughty et al., 2016; Murphy et al., 2021; Roman et al., 2014). The changes in productivity in turn feedback to affect food availability for marine mammals. 4. *Ocean phytoplankton productivity forms feedbacks with climate processes.* Phytoplankton productivity affects ocean biogeochemical cycles and carbon budgets, air-sea gas exchanges, and upper ocean albedo and radiation budgets (e.g., Arrigo et al., 1999; Lim et al., 2019; Manizza et al., 2008; Tian, Zhang, & Wang, 2021; Tian, Zhang, Wang, & Zhi, 2021). These affect climate-ocean feedbacks, and generate feedbacks on ocean productivity (e.g., Behrenfeld, O'Malley, et al., 2006; Falkowski et al., 1998; Henson et al., 2022; Kohfeld et al., 2005). Ocean currents or organism movement results in spatial transfers of production connecting remote ecosystems, creating further feedbacks involving local productivity. 5. *Forest ecosystem processes generate feedbacks with regional and global climate processes.* Forests are globally important carbon stores affecting atmospheric $CO_2$ levels and climate processes (e.g., vegetation albedo affects regional radiation budgets; Flores & Staal, 2022; Li et al., 2022; Zhang, Hao, et al., 2022). Forests influence regional water cycles affecting weather patterns and precipitation levels, water storage, and atmospheric exchanges through evapotranspiration, which in-turn feedback on forest ecosystem processes (e.g., Guz & Kulakowski, 2020; Jiao et al., 2021; Li et al., 2022; Lima et al., 2014). Consequently, deforestation can impact all of these aforementioned processes (Li et al., 2022; Lima et al., 2014). 6. *Large herbivore grazing generates feedbacks involving water cycles and carbon storage.* Bison and other large herbivores graze vegetation, recycle nutrients and maintain biological diversity, which can increase ecosystem resilience, enhance carbon storage, and modify the physical structure of the land to store more water (e.g., Doughty et al., 2016; Ling et al., 2023; Malhi et al., 2022; Zhu et al., 2023). Many species also undertake large seasonal migrations, transferring nutrients and affecting regional scale ecosystem structure and functioning, which in-turn affects the capacity of the habitat to support populations of large herbivores (e.g., Anderson et al., 2024; Doughty et al., 2016; Geremia et al., 2019; te Beest et al., 2016). Such landscape-level development generates feedbacks involving regional and global climate processes.

In the following sections, we focus on three aspects of ecological feedbacks that are central to understanding their role in the Earth system and in future model development (Figure 1): (a) ecological feedbacks between biotic elements within ecosystems, (b) ecological feedbacks with the physical environment, and (c) ecological feedbacks with biogeochemical processes, providing examples to illustrate the operation and importance of ecological feedbacks (see also Table S1 in Supporting Information S1). We also note that many of the highlighted feedback cycles may also be important in broader interaction cycles influencing ecosystem, physical, biogeochemical, or climate processes.

## 3. Ecological Feedbacks Between Biotic Elements Within Ecosystems

Biotic interactions are those that occur between different species or individuals of the same species and may be direct or indirect (via other species or environmental processes; Fraser et al., 2021). Interactions between organisms may be positive, negative, or neutral, and include grazing (consumer-resource), competition, predator-prey, facilitation, mutualism, commensalism, and parasitism. Such biotic interactions can form pathways connecting organisms and are important in generating different types of ecological feedback cycles (Pichon et al., 2024; Sih et al., 2011). Individual species, a particular set of species, or the overall diversity of species can be important for nutrient recycling, productivity, carbon storage, vegetation community structure, food web interactions, or the abundance of other species within an ecological community (Burkepile & Thurber, 2019; Hector & Loreau, 2005; Jones et al., 1997; Murphy et al., 2016; Shannon et al., 2023). In this section, we highlight examples of biotic interactions within ecosystems that form feedback cycles (see also Table S1 in Supporting Information S1).

Biotic feedback cycles occur through interactions where one species uses another for its advantage, such as predator-prey, producer-grazing, or parasite-host interactions. In producer-grazing interactions, grazing by herbivorous or omnivorous species can be a major determinant of the standing stock of primary producers. For example, grazing by zooplankton in oceanic systems is a key process during the spring development of upper ocean phytoplankton blooms affecting the magnitude and duration of bloom conditions (Karakus et al., 2022; Nissen et al., 2018; Sunda & Shertzer, 2012, 2014). As these blooms develop, increases in zooplankton abundance and grazing pressure reduce the concentration of phytoplankton, which in-turn leads to the decline in zooplankton abundance (negative feedback), allowing a recovery in phytoplankton concentration (positive feedback; Chenillat et al., 2021; McCreary et al., 1996; Sunda & Shertzer, 2014). Such feedback cycles can influence breeding success, species' spatial distributions, and lead to a range of complex interactive population dynamic outcomes, including stable population levels, population cycles, and apparent chaotic variations (Bauer et al., 2013; Lima et al., 2002; Mandal et al., 2006; Ray et al., 2001). The same types of feedback are observed across food webs in terrestrial systems, such as grasslands, where grazing by large herbivores, such as bison or deer, can lead to reductions in food availability, driving competition and initiating dispersal to new foraging areas or potential population declines (Geremia et al., 2019; Ling et al., 2023). Host-parasite interactions can also form feedback cycles of linked population increases and decreases that are a fundamental aspect of ecological networks (Holmquist et al., 2023; Hudson et al., 1998).

Competitive relationships between species form indirect feedback cycles, involving access to nutrients, prey, space, or other resources. Gains for one species may lead to losses for another, allowing further gains for the more competitive species (positive feedback), with knock-on effects to the wider food web. Examples include the relative success of different zooplankton species grazing on various phytoplankton groups (e.g., diatoms or cyanobacteria) or fish feeding on zooplankton groups (e.g., copepods or amphipods; Hashioka et al., 2013; Sailley et al., 2013). These processes are part of dynamic networks of interactions, for example, competition between grazer groups of migratory Serengeti herbivores (zebra, wildebeest) also facilitates grazing by other groups (gazelle; Anderson et al., 2024).

Movements of organisms can also result in biotic interaction feedback cycles within and between ecosystems. For instance, grazing by bison is an important determinant of the wave of spring growth in grassland ecosystems (the Green Wave), affecting seasonal grassland development, which can positively impact grazing conditions (Geremia et al., 2019). Animal movements (such as migrations) also connect food webs resulting in a spatially and temporally variable mosaic of biotic interaction networks, which can lead to feedback cycles and influence the structure and functioning of the connected ecosystems (see the next section; Bauer & Hoye, 2014; Malhi et al., 2022; Murphy et al., 2021; Pease, 2024).

Biotic interactions involved in feedback cycles do not occur in isolation from each other or the environment. For example, vegetation changes in terrestrial ecosystems may involve fluctuations in plant community structure and/or biogeochemistry, with processes involving multiple species and chemical pathways (Pugnaire et al., 2019; Verheijen et al., 2015). The full range of biotic interactions underpinning food webs (Pichon et al., 2024) generates feedbacks in ecological networks that affect the distribution and abundance of species, and are crucial in maintaining the overall structure and functioning of ecosystems. These interactions can span the entirety of the food web, with changes in plant abundance and diversity impacting sediment dwelling microbes (Fox et al., 2020; Li et al., 2020, 2021) and top predators (Hammerschlag et al., 2019). Further, many species can have a disproportionate impact on ecosystems through modulating resource availability (often referred to as "ecosystem engineers"). For example, by building dams, beavers influence where nutrients are deposited in streams and the extent of surrounding wetlands, which can in turn impact water quality and the recruitment of aquatic plants (Brazier et al., 2021). The influence of such species on resource availability generates feedbacks, changing environments, community structure, and the functioning of ecosystems (Grenfell et al., 2019; Peller et al., 2022; Rilov et al., 2023; Sanders et al., 2014; Zhong et al., 2022).

The multi-level trophic interactions within food webs that generate top-down and bottom-up effects can, in turn, impact ecosystem functioning and the resilience of ecosystems and responses to change (Hooper et al., 2005; Peller et al., 2022; Reid et al., 2000; Ren et al., 2022). Such species interactions generate higher-level emergent properties (e.g., food web structures, seasonal food web dynamics, spatial patterning and structure) within and across ecosystems, involving multiple feedbacks (Bauer & Hoye, 2014; Fulton et al., 2019; Losapio et al., 2023; Pichon et al., 2024; Wang et al., 2021). For instance, grazing by large animals in grassland ecosystems may enhance grazing conditions in a positive feedback cycle, but can also promote complexity of trophic webs, habitat heterogeneity, and enhance plant dispersal, increasing resistance to abrupt ecosystem change through microclimate modification (e.g., Geremia et al., 2019; Malhi et al., 2022).

Feedback cycles in ecological networks vary in strength, involve multiple time scales, and can generate rapid changes, with cascading effects across trophic levels (Dutkiewicz et al., 2021; Gil et al., 2020). Tipping points are the instance at which an incremental change triggers extensive reorganization of a system's structure and function (Armstrong McKay et al., 2022). If the subsequent effects of reaching a tipping point destabilizes the food web, it can have knock on effects on ecosystem functioning (Armstrong McKay et al., 2022; Ban et al., 2022). An example of this is the destruction of kelp forest ecosystems off the west coast of North America due to the loss of a key feedback cycle: declines in the sea otter population, the main predator of sea urchins, resulted in the ecological release of urchin populations, which allowed urchins to destroy entire kelp habitats (Smith, Tomoleoni, et al., 2021). Kelp habitats are some of the most productive ecosystems in the world and important for biodiversity, fisheries, tourism, carbon sequestration, and wave attenuation (Krause-Jensen & Duarte, 2016; Leichter et al., 2023; Zhu et al., 2022). Thus, the loss of these interactions and feedbacks had multiple ramifications for biodiversity, biogeochemical cycling, and ecosystem functioning (Krause-Jensen & Duarte, 2016; Leichter et al., 2023). Similarly, within the Brazilian Atlantic Forest, the integrity of vertebrate communities is relatively stable up until 60% habitat loss, but at ~70% habitat loss a tipping point is reached, leading to nearly complete species turnover (Banks-Leite et al., 2014).

The above studies illustrate how ecological interactions and feedbacks can shape ecosystem structure, functioning, and responses to change, leading to the recognition of ecosystem stability, a key ecological concept that has developed over the last half century (Van Meerbeek et al., 2021). Early work emphasized the role of ecological feedbacks for ecosystem stability through deterministic models of ecological interactions that identified stable points and basins of attraction in equilibrium systems. Over time, the concept has developed, recognizing the complex nature of ecological systems (including non-equilibrium systems) and the multiple influences on their structure and functioning (Donohue et al., 2013, 2016; Van Meerbeek et al., 2021). Ecological feedbacks are now recognized as fundamental in determining ecosystem resistance and resilience, two properties critical to determining ecosystem stability (Capdevila et al., 2021). For example, across numerous systems, species diversity, redundancy, and complementarity are all thought to enhance resistance to and recovery from perturbation (Palumbi et al., 2008). This diversity effect, at least in response to biological invasions however, is thought to be stronger in terrestrial systems than marine (Kimbro et al., 2013). Recent studies have emphasized the need for an integrated conceptual framework to better understand ecosystem stability and associated properties (Capdevila et al., 2021; Van Meerbeek et al., 2021).

## 4. Ecological Feedbacks With the Physical Environment

Interactions and feedbacks between ecological processes and the physical environment determine key aspects of physical process operation and structure in the Earth system (Armstrong McKay et al., 2021; Ehrenfeld et al., 2005; Foley et al., 2003; Hense et al., 2017). Animal and plant species can determine the physical structure of a habitat, such as the geomorphology of coastal regions and associated sediment dispersal, which can affect other abiotic processes, such as hydrological cycles, ocean circulation, and microclimate (De Frenne et al., 2021; Milling et al., 2018). The loss of such ecological systems following changes in the Earth system can lead to complex cascading effects (Barbier et al., 2011; Jones et al., 1997). In this section, we highlight examples of the interactions between ecological and physical processes that generate feedback cycles (Table S1 in Supporting Information S1).

Within terrestrial ecosystems, a prime example of ecological–abiotic feedbacks are plant-soil-microbe feedbacks. The physical and chemical properties of soil (moisture, temperature, pH, and structure) fundamentally underpin the quality of a plant's environment (van der Putten et al., 2013) as well as the quality of the environment for diverse communities of microbes (e.g., bacteria and fungi) that live in the soil (Ren et al., 2018). In turn, plants and microbes change these properties through growth and metabolism. For instance, plants reduce soil moisture through evapotranspiration, while limiting direct soil evaporation through the insulating effects of litter, shade created by the plant canopy, and by modulating surface temperature through changes in surface albedo (Ehrenfeld et al., 2005). These moisture feedbacks can also drive changes in plant communities (Gao et al., 2023) and microbial communities (Li et al., 2020). Over longer timescales, such feedbacks can drive succession and, for example, create features like tiger bush vegetation (banded patterns of plants separated by areas of lower plant cover or bare ground) in arid and semiarid ecosystems (Puigdefábregas, 2005).

In aquatic environments, ecological processes involving benthic ecosystems can affect water clarity and sediment properties. Taking shallow lakes as an example, feedbacks can occur between clarity (and turbidity) and benthic macrophyte and invertebrates, while in shallow coastal regions, feedbacks associated with seagrass presence can result in reduced suspended sediment concentrations, increased light levels, and enhanced growth rates (Blindow et al., 2014; Holker et al., 2015; Jeppesen et al., 1997). Coastal vegetation (e.g., mangroves, saltmarshes, or seagrasses) and benthic communities can affect local hydrodynamics and stabilize sediments, resulting in the development of larger-scale physical structures (e.g., dune complexes and areas of salt marsh), in positive feedback cycles (de Smit et al., 2022; Marin-Diaz et al., 2020; van de Ven et al., 2024). Ecological feedbacks between organisms and sediment processes can result in stabilization (e.g., binding microbial processes) or destabilization (e.g., disturbing macrofauna) affecting hydrodynamics and rates of sedimentation, erosion and transport (Bianchi et al., 2021; Dairain et al., 2020; Harris et al., 2015; Hillman et al., 2020).

In oceanic systems, ecological and physical processes interact to affect upper ocean radiation budgets (Tian, Zhang, & Wang, 2021; Tian, Zhang, Wang, & Zhi, 2021). Light absorption by phytoplankton affects surface ocean mixed-layer temperatures, stabilization, and albedo—the proportion of incident solar radiation reflected by a surface (Hense et al., 2017). In a positive feedback cycle, increased phytoplankton concentration enhances stabilization of the water column, maintaining the plankton at shallower depths where light conditions and hence growth conditions are more favorable. Changes in upper ocean stabilization affect upper ocean circulation and ocean-atmosphere interaction (Hense et al., 2017; Loptien et al., 2009; Paulsen et al., 2018; Tian, Zhang, & Wang, 2021). Such physical changes not only impact phytoplankton growth rates, but can also affect interactions involved in feedbacks within plankton communities (e.g., zooplankton grazing on phytoplankton) and hence the dynamics of phytoplankton communities and further interactions with ocean physical processes (Heinemann et al., 2011).

Albedo feedbacks are also crucial on land, where vegetation cover strongly influences surface reflectivity and local climate (Bonan et al., 2024). Albedo varies across ecosystems and seasons depending on factors such as leaf color, canopy density, and ground exposure, and cloud cover generated through evapotranspiration (Bonan, 2008; Richardson et al., 2013; Suni et al., 2015). When vegetation cover changes due to natural or anthropogenic drivers, the resulting shift in albedo can alter surface energy absorption and temperature, reinforcing further ecological change. For example, in Arctic tundra, reindeer preferentially graze on shrubs, which reduces shrub abundance. Since shrubs absorb more sunlight than snow or grasses, this loss increases surface reflectivity (summer albedo), which can have a cooling effect on the local Arctic climate (te Beest et al., 2016). If this cooling is strong enough to further impair shrub growth, it could trigger a positive feedback loop. In snow- and icedominated ecosystems, biological activity can reduce albedo: algal blooms, cryoconite (dust–soot–cyanobacteria aggregates), and dense ice worm populations darken the surface, which leads to warming and accelerates snow and ice melting (Hotaling et al., 2021; Yallop et al., 2012).

Tightly linked to albedo effects on the surface energy balance is evapotranspiration, the primary mechanism by which vegetation recycles water and cools the land (Bonan et al., 2024). This effect is particularly strong in tropical forests, such as the Amazon, where dense vegetation sustains high transpiration rates, maintaining atmospheric moisture, supporting convective rainfall, and reinforcing forest productivity through a self-reinforcing feedback loop (Gentine et al., 2019; Spracklen et al., 2018). Conversely, deforestation reduces transpiration, leading to drier conditions, less cloud cover, higher surface temperatures, and decreased rainfall (Figure 3), which can further stress vegetation and alter regional climate patterns (e.g., Betts et al., 2004; Bonan et al., 2024; Butt et al., 2023). In arid regions, Charney (1975) hypothesized that reduced vegetation cover increases albedo and decreases evapotranspiration, reinforcing desertification in a positive feedback.

Complementing albedo and evapotranspiration effects, vegetation also modifies surface roughness, with taller and more complex canopies enhancing turbulent mixing, promoting convective activity, and modulating local temperatures (Schnabel et al., 2025; Winckler et al., 2019; Wulfmeyer et al., 2014). Roughness has been identified as a leading biophysical driver of surface temperature variability between forested and deforested regions in the eastern United States (Burakowski et al., 2018) and could trigger convection and rainfall above simulated plantations in desert ecosystems (Wulfmeyer et al., 2014). These roughness effects interact with albedo and evapotranspiration in a way which is critical for ecosystem stability: for instance, large-scale rainforest loss can push systems like the Amazon toward a tipping point, potentially converting it to savanna or seasonal dry forest (Lenton et al., 2023; Steffen et al., 2018).

Plants also facilitate feedbacks involving fire, as some plants use fire cues such as high temperature and smoke to trigger germination and synchronize flowering (Ramos et al., 2019; Wagenius et al., 2020). Fire regimes shape the structure and composition of ecosystems and control the distribution and diversity of biomes (Foley et al., 2003; McLauchlan et al., 2020; Pausas & Keeley, 2009; Pausas & Ribeiro, 2013). These plant-fire interactions feedback on atmospheric properties, weather, and plant trait distributions, which in turn determine the ecosystem flammability and thus impact the prevailing fire regime (frequency, intensity, size, season, spread type, and extent; Archibald et al., 2018). In sub–Saharan Africa during low rainfall regimes, tree growth is limited by water availability and savannas arise. In high rainfall regimes, the canopy closes and forests prevail (Staver et al., 2011a). When tree cover is below 50%, a continuous grass layer promotes fires and prevents trees from establishing, maintaining the savanna. Above this threshold, tree cover becomes increasingly competitive, suppressing fires (it is harder for fire to penetrate forest), and eventually enabling canopy closure. As a result, forests and savannas both persist and tree cover is bimodal, indicating that savanna is a distinct and possibly alternative stable state to forest (Staver et al., 2011b). Reproducing this phenomenon within dynamic global vegetation models has proven difficult (Hopcroft & Valdes, 2022), highlighting the complexity of these ecological processes. Past research has suggested that model improvements could be made by including a fuller representation of plant functional types along with dynamic fire disturbance (Hopcroft & Valdes, 2022), and there may also be additional underlying influences playing important roles in vegetation feedbacks, such as herbivory, human intervention, and soil properties (D'Onofrio et al., 2020; Sankaran et al., 2005; Claussen et al., 2013). Forest fires can also change surface radiative budgets, affecting surface temperature through changes in albedo and evaporative cooling (Liu et al., 2005).

Through their movement, foraging patterns, reproductive behavior, and social interactions, animals play key roles in ecosystem functioning (Hammerschlag et al., 2019; Malhi et al., 2022). At forest edges, such as in a fragmented landscape caused by deforestation, boundary effects have an impact on animal behavior, as forests adjacent to open areas are hotter, drier, and more exposed to wind than forest interiors (Ewers & Banks-Leite, 2013; Laurance & Curran, 2008; Murcia, 1995). These changes in microclimatic conditions also trigger shifts in plant communities at forest edges, ranging from higher mortality of trees, lower recruitment of seedlings, and increased turnover rates from climax to early successional species, which leads to the secondarisation of forest edges (Laurance, Ferreira, et al., 1998; Laurance, Laurance, & Delamonica, 1998; Tabarelli et al., 2008). Animal species can avoid edge habitats as a direct response to increased light, but most do so indirectly through the abiotic-driven changes in plant communities (Banks-Leite et al., 2010; Patten & Smith-Patten, 2012). Thus, there is positive feedback between changes to abiotic conditions and plant and animal communities, which means that in highly human-modified landscapes, the magnitude (e.g., intensity) and extent (e.g., width) of edge effects increases through time and can eventually become the dominant habitat.

## 5. Ecological Feedbacks With Biogeochemical Processes

Life on Earth influences the cycling of chemical elements, including the ability of land, freshwater, or ocean to be a net sink or source of a certain gas, which often changes over seasonal cycles. There are extensive ecological feedbacks within ecosystems affecting biogeochemical and nutrient cycling, primary production, and carbon storage. These include trophic interactions (see above) that can affect levels of primary production and hence biogeochemical cycles and carbon budgets (Table S1 in Supporting Information S1). The movement and behavior (e.g., aggregations or migrations) of organisms can also have large impacts on carbon cycling, concentrating nutrient input at specific times and/or places. Ecosystems also influence atmospheric gaseous concentrations, such as through the release of biogenic volatile organic compounds (BVOCs), nitrogen oxides ($NO_X$), or $CO_2$. In the following section, we highlight some of the diverse ways in which ecological processes interact with biogeochemical processes in ecological feedback cycles.

A major area where the crucial role of ecological feedbacks in the Earth system has been recognised and explored is the global carbon cycle (Friedlingstein, 2015; Friedlingstein et al., 2006). Ecological feedbacks influence land and ocean carbon exchanges with the atmosphere that are crucial in determining the concentration of atmospheric $CO_2$ and the fate of anthropogenically-derived $CO_2$ (Bonan & Doney, 2018; Fisher et al., 2014; Walker & Palevsky, 2025). For example, in terrestrial ecosystems, photosynthesis absorbs $CO_2$ from the atmosphere, while respiration and decomposition result in the release of $CO_2$ back to the atmosphere. Carbon is stored as vegetation (e.g., leaves, woody material, and roots) and as organic matter in the soil (e.g., litter), and whether the ecosystem is a source or sink of atmospheric $CO_2$ depends on the balance of the uptake, recycling, and loss processes (Bonan & Doney, 2018; Bonan et al., 2024). These processes vary across different types of ecosystem (e.g., forests, savanna and grasslands) and environments (e.g., different types of tropical, temperate or boreal forests). Higher atmospheric $CO_2$ levels has caused increases in global primary productivity, where $CO_2$ fertilization has led to increased photosynthesis/plant growth (Walker et al., 2020). This highlights the important role of ecological feedbacks in the evolution of anthropogenically-driven climate change. To appreciate the net effect and direction of this carbon feedback, a better understanding of which portion of the change is respired back to the atmosphere is needed (Quetin et al., 2023). Sensitivity of photosynthetic metabolism to increasing temperatures is, however, a large source of uncertainty in climate-carbon cycle feedbacks (Booth et al., 2012). Another source of sensitivity is the definition of the plant-carbon-nitrogen relationship; in dynamic vegetation models, insufficient representation of competition between deciduous versus evergreen and trees versus grass over the tropics and subtropics drives biased vegetation cover with warming and causes an increase in respiration of carbon back to the atmosphere (Sakaguchi et al., 2016). Furthermore, current global vegetation models lack thorough representation of plant succession and community organization (see Bonan et al., 2024 and references therein).

Within the upper ocean, the balance of $CO_2$ uptake and loss affects $CO_2$ concentration and hence ocean-atmosphere exchanges (Bonan & Doney, 2018; Friedlingstein, 2015; Friedlingstein et al., 2006; Hense et al., 2017). Termed the biological pump, phytoplankton in the high light environments of the upper ocean take up $CO_2$ during photosynthesis, and some of that carbon is exported into the deeper ocean through the sinking of organic material or via transfers associated with the vertical migration of organisms (Getzlaff & Kriest, 2024; Jonasdottir et al., 2015). Carbon is released back into the ocean through respiration and breakdown of organic material (e.g., through microbial processes and grazing interactions; Cavan & Boyd, 2018; Cavan et al., 2019). Particulate carbon exported from the upper ocean may be transported in ocean currents, stored through burial in sediments in shelf and deeper ocean areas, or recycled through microbial processes (Boyd et al., 2019). It is thought that without this ecological and biological carbon pump, there would be around 50% more $CO_2$ in the atmosphere (Knox & McElroy, 1984; Sarmiento & Toggweiler, 1984; Toggweiler, 1999). Ecological processes are also important in the carbonate pump (Hense et al., 2017), through the formation of calcium carbonate ($CaCO_3$) in the generation of hard structures such as shells or coral reefs. These processes, and the associated ecological feedbacks, vary across the world ocean, and alongside physical processes affecting $CO_2$ changes (the solubility pump), results in regions differing in the net direction of $CO_2$ transfer.

Coral reefs are a well-documented example (Figure 2), where both autotrophic production and calcification influence local ocean carbon chemistry over multiple time scales with climate feedbacks on atmospheric $CO_2$

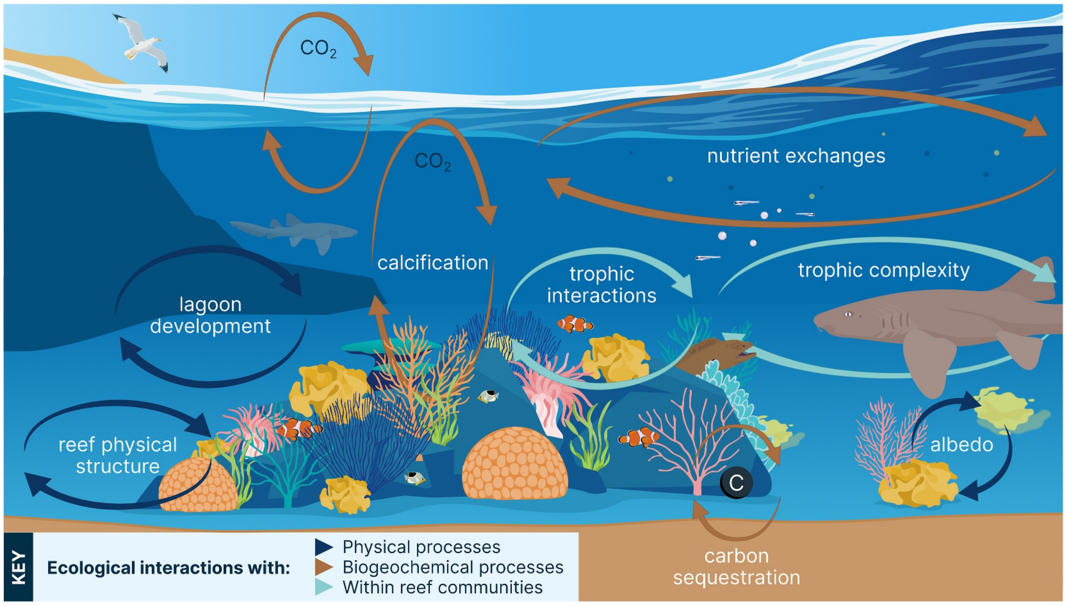


**Figure 2.** Examples of the diverse range of ecological feedbacks influencing the functioning of coral reef systems, involving ecological interactions with physical and biogeochemical processes. *Physical processes:* The growth of structurally complex coral reefs (reef physical structure) modifies water circulation, affecting patterns of ocean circulation, shoreline development (e.g., lagoon formation and shoreline protection from storms), which can further enhance reef development (Barbier et al., 2011; Corbera et al., 2022). Benthic community structure in reef areas influences benthic albedo, and radiation budgets can generate access to refuges for vertebrate and invertebrate communities, and can also act as a source of biogenic aerosols (BVOCs) affecting local atmospheric properties (Jackson et al., 2018; Mishra et al., 2007). *Biogeochemical processes:* Formation of reefs in low nutrient regions can generate areas of enhanced biogeochemical cycling, and lead to further reef and ecosystem development. Nutrient transfers through ocean currents and animal movements associated with reef ecosystems can enhance primary productivity, which in turn supports reef food webs, reef ecosystem development, biodiversity, and resilience, which involve extensive ecological feedbacks (Williams et al., 2018). Calcification/dissolution processes (influenced by ocean pH) and productivity of corals and associated ecological communities affect upper ocean carbon budgets and carbon sequestration, and in turn atmosphere-ocean carbon exchanges and hence climate (Anthony et al., 2011). Within reef communities: biotic interactions, such as predator-prey, competition, mutualism, or parasitism, generate direct (two-way between organisms) and indirect (via other organisms or the environment) feedback cycles (Pichon et al., 2024; Sih et al., 2011).

(Anthony et al., 2011; Bouttes et al., 2023; Rockstrom et al., 2009). Coral-associated algae photosynthesis decreases the partial pressure of $CO_2$ ($pCO_2$), allowing more $CO_2$ to dissolve into the ocean surface from the atmosphere, whereas calcification (associated with coral growth) increases $CO_2$. The balance of organic-to-inorganic carbon production, or photosynthesis to calcification, is the principal driver of whether the reef acts as a net sink, or more commonly, a net source of atmospheric $CO_2$. Ecological controls on this balance, and therefore local atmospheric $CO_2$ fluxes, include community composition (Anthony et al., 2011; Bouttes et al., 2023; Mumby, 2009), microbial diseases that can decrease coral cover (Aronson & Precht, 2001; Hughes, 1994), abundance of coral or algal grazers (Gil et al., 2020; Mumby, 2009; Wabnitz et al., 2010), and coral community predator-prey interactions (Gil et al., 2020), with abiotic influences including ocean circulation (Lonborg et al., 2019), extreme atmospheric events (Madden et al., 2023), and nutrient supply (Lowe & Falter, 2015).

Nutrient availability indirectly impacts climate as it can regulate primary productivity, which impacts whether a system is a net source or sink of $CO_2$. Organisms can change local nutrient conditions, through nutrient uptake and release, and through localized movements, aggregation, and/or migration behavior (as discussed above; Bauer & Hoye, 2014). In terrestrial ecosystems, soil microbes and plants are involved in chemical feedbacks, which typically involve complex mechanistic pathways that affect soil pH, redox processes, and carbon-, nitrogen- and micronutrient-cycling and can act over timescales of decades to millennia (Bardgett et al., 2008; Ehrenfeld et al., 2005; Patoine et al., 2022). Plant-induced accumulation of soil organic carbon in the early stages of succession for example, can create "islands of fertility," which provide a better environment for plant growth in

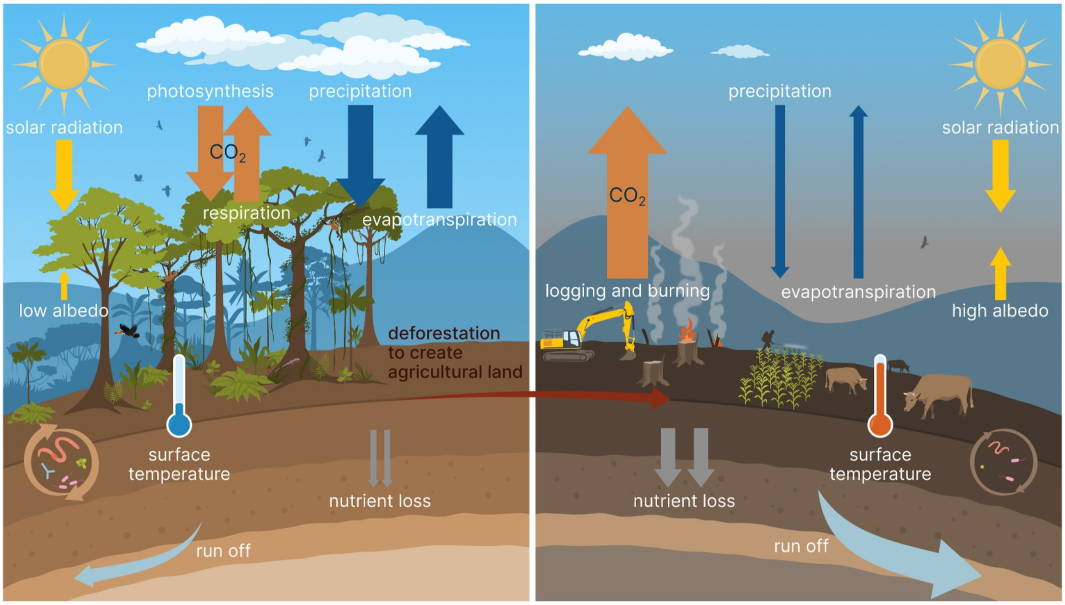


**Figure 3.** Deforestation disrupts biophysical and biogeochemical processes that are underpinned by ecological feedbacks. Ecological feedbacks have a crucial role in the maintenance of forest ecosystems and are disrupted through deforestation of a healthy tropical forest area when it is transformed for agriculture (Flores & Staal, 2022; Li et al., 2022). These feedbacks include ecological processes involved in climate regulation, water cycles, above-ground carbon fluxes, and soil properties. For example, loss of vegetation cover in tropical and temperate regions can lead to a drier climate, further warming, reduced precipitation, and more forest loss (Butt et al., 2023). These processes involve complex interactions, with outcomes varying latitudinally and regionally, which in turn affects local and global climate (Lawrence et al., 2022). Aspects of these feedbacks are included in current Earth system models, but many of the underlying ecological processes involved are not resolved (e.g., aspects of vegetation community dynamics, microbial system processes, trophic interactions, soil-vegetation structure and dynamics, or cross scale interactions in ecosystems).

general, leading to the further accumulation of soil carbon (Berendse, 1998). In the ocean, secondary production can also be enhanced by regenerated nutrients, for example, Antarctic krill may stimulate surface primary production by releasing ammonia whilst they graze on phytoplankton (Atkinson & Whitehouse, 2000; Cavan et al., 2019; Whitehouse et al., 2011).

There is growing appreciation of the contribution that some species make to microclimate modifications by acting as nutrient vectors (Malhi et al., 2022). Numerous cross-taxa evidence suggests that aggregating and migratory organisms have a pulsing (intense, short-term) impact on biogeochemical cycling, primary productivity, and ecosystem functioning (Bauer & Hoye, 2014). One example of this is the mass drownings of wildebeest (*Connochaetes taurinus*) that occur during their annual migration, which provides a substantial input of nutrients into the Mara River and can greatly influence the food webs and nutrient cycles within the river ecosystem (Subalusky et al., 2017). Within the oceans, it has been suggested that through consuming prey in offshore pelagic waters and then egesting material over coral reef ecosystems, grey reef sharks (*Carcharhinus amblyrhynchos*) may contribute substantially to nutrient transfer, providing subsidies that are important for the health of nutrient-limited coral reefs (Williams et al., 2018). Further, seasonally migrating copepods can transport carbon to the deep ocean when they enter a state of diapause in the deep ocean over winter (Jonasdottir et al., 2015), while diurnal migration of zooplankton and fish is also important in the annual export of carbon from the surface layer (Getzlaff & Kriest, 2024). Swarms of migrating marine animals can also mix nutrients, as has been shown for jellyfish (Katija & Dabiri, 2009) and suggested in Antarctic krill (Cavan et al., 2019).

Ecosystems are a source of BVOCs to the atmosphere. These compounds play important roles within plants (growth, development, reproduction, stress response), between plants (airborne signals), between plants and other organisms (direct and indirect defense, attractors; Burakowski et al., 2018; Peñuelas & Staudt, 2010). They also modulate the chemical composition and physical characteristics of the atmosphere at the local, regional, and global scales. The net effects of BVOCs on climate are difficult to predict as they are sensitive to the state of the atmosphere. For example, BVOCs released from plants can directly affect ozone concentrations; in urban areas, the oxidation of BVOC (e.g., isoprene) can stimulate ozone production, but in less urbanized area (low atmospheric NOx) BVOCs oxidation can reduce ozone concentrations (Collins et al., 2002; Hofzumahaus et al., 2009). Other climatic influences of BVOCs released by plants include increasing the lifetime of methane in the atmosphere, which can contribute to atmospheric warming, and the formation of secondary organic aerosols that act as cloud condensation nuclei increasing sunlight reflection from low clouds and leading to atmospheric cooling (Burakowski et al., 2018; Claeys et al., 2004; Collins et al., 2002; Hofzumahaus et al., 2009).

## 6. Implications

### 6.1. Ecological Implications of Changes to Ecological Feedbacks

Exploitation by humans of natural resources and anthropogenically-driven global environmental changes are affecting the structure and functioning of ecosystems, which in turn can affect nature's capacity to maintain biological diversity and provide services that are crucial for human societies and the Earth system (Barnosky et al., 2012; IPBES, 2019; IPCC, 2022). These anthropogenic impacts have accelerated over the last century, degrading ecological systems (IPBES, 2019). Within terrestrial and freshwater realms, habitat destruction through deforestation and agricultural and urban development has resulted in large changes to habitat characteristics, ecological community composition, and ecosystem functioning (Figure 3; Allan, 2004; Newbold et al., 2015). In the marine realm, harvesting, industrial development, pollution, and transport have resulted in major shifts in ecosystem structure and functioning, particularly in many of the most productive, diverse, and complex oceanic ecosystems (IPCC, 2019; United Nations, 2021).

Concurrently, ecosystems are simultaneously affected by climate change (IPBES, 2019; IPCC, 2022; United Nations, 2021). The result is that organisms are often impacted by multiple stressors within their environment, with the exact combination varying between local and regional systems (IPCC, 2022; Kroeker et al., 2017). Despite many ecological effects manifesting locally or regionally, the combined impacts of these disruptions and the subsequent change of ecosystem functioning, is occurring at a planetary scale (Archibald et al., 2018; IPBES, 2019; IPCC, 2022; Sala et al., 2021). One way in which plant and animal species are responding to climate change is by shifting their ranges (IPBES, 2019; IPCC, 2022; United Nations, 2021). These range shifts are leading to a proliferation of species invasions and novel ecological communities that may influence climate and biosphere feedbacks via multiple mechanisms, including changes in albedo, biologically-driven carbon sequestration from the atmosphere to the deep sea, and the release of greenhouse gases (Heneghan et al., 2023; O'Connor et al., 2021; Pecl et al., 2017; Ren et al., 2022).

These anthropogenic-driven changes are making it harder to understand and model already complex ecological feedbacks. For example, predicting carbon flow at ecosystem scales is made even more challenging by the impact of human disturbances on feedbacks involving microbes. On coral reefs, global increases in fleshy algae and other photosynthetic organisms, due to multiple anthropogenic perturbations, can cause an increased release of dissolved organic carbon (DOC) into the water column. This DOC can support increased microbial biomass, with potential increases in diseases from pathogenic bacteria threatening corals and ultimately favoring algal growth (Haas et al., 2016; Silveira et al., 2017). There is also a switch in the dominant pathway for carbohydrate breakdown to a more energy intensive pathway which increases the risk of hypoxia from the bacterial respiration of DOC and release of $CO_2$ (Haas et al., 2016). This process is known as microbialisation and can create a feedback cycle of coral death, algal overgrowth and regime shifts, and more microbial biomass (Dinsdale & Rohwer, 2011; Haas et al., 2016; Rohwer et al., 2002). This in turn keeps resources locked in the microbial compartment of the reef, at the expense of higher trophic levels, and can cause the overlying water to become depleted in oxygen due to increased microbial respiration (Silveira et al., 2019). Microbilisation could fundamentally change the biogeochemical fluxes on reefs, and elsewhere, but is currently hard to predict based on a lack of understanding of the complexity of interactions at play.

The simultaneous operation of multiple feedbacks in ecosystems can result in widespread secondary impacts in response to change (O'Connor et al., 2021). Alterations of forest ecosystems, such as the deforestation within the Amazon rainforest for agricultural expansion or infrastructural development, can affect the spatial structure of the ecosystem and land-atmosphere feedbacks at a regional scale (Butt et al., 2023; Flores & Staal, 2022; Longo et al., 2018). Perturbations in regional scale feedbacks can then change large scale atmospheric circulation patterns, resulting in changes in rainfall patterns and, consequently, shift the water balance of river basins (Lima et al., 2014; Smith et al., 2023). Changes in the water balance, especially extreme events such as floods and droughts, or by the damming of waterways (Maavara et al., 2020), can impair forest ecosystem services, such as provision of nutrients and habitat suitability for many species at local scales (Coe et al., 2013; Lima et al., 2014). Such ecological feedbacks can also generate connections over large scales by influencing atmospheric processes—termed ecoclimate teleconnections—which can impact ecosystems that are remote from the original system (e.g., Garcia et al., 2016; Swann et al., 2012, 2018). Analyses of the larger atmospheric impacts of more localized ecological feedbacks has so far concentrated on forest ecosystems and their influence on regional and global scale atmospheric circulation (Bonan et al., 2024; Garcia et al., 2016). Ecoclimate teleconnections also operate in oceanic systems, for example, plankton derived dimethylsulfide (DMS) influences cloud nucleation and regional atmospheric processes, while feedbacks between upper ocean planktonic ecosystems and ocean-atmosphere processes influence atmospheric dymanics across the Pacific Ocean, including the El Niño-Southern Oscillation (ENSO), generating large scale remote impacts (Jochum et al., 2010; Paulsen et al., 2018; Tian, Zhang, & Wang, 2021; Tian, Zhang, Wang, & Zhi, 2021; Tian et al., 2019; Xu et al., 2016).

Much of the focus of past research has been on the responses of ecological systems to environmental change—that is, environmental changes are usually considered as "external drivers" to which organisms or biological systems respond (Bonan & Doney, 2018). However, due to feedbacks, ecological changes resulting from environmental changes can then impact the structure and functioning of ecosystems, with knock on effects for the ecosystem's stability and resilience to anthropogenic impacts (IPBES, 2019; Liang et al., 2022; O'Connor et al., 2021; Verburg et al., 2016). Ecological responses to change involve multiple, and often complex, pathways of ecological-physical-biogeochemical interaction, generating feedbacks on a range of times scales (from days to centuries or millennia) and spatial scales (local, regional and global, Table S1 in Supporting Information S1; Figure 4). For example, in high-latitude polar regions, atmospheric warming and loss of ice shelves exposes new areas of ocean surface, enhancing productivity and carbon storage in sediments, and acting as a potential negative feedback on atmospheric warming (Peck et al., 2010). Atmospheric warming and increased $CO_2$ concentrations can also affect plant productivity and carbon storage in terrestrial ecosystems across the world (Jiang et al., 2020; Muller et al., 2016), generating complex feedbacks that add additional uncertainty to assessments of the impacts on carbon budgets and atmospheric processes.

### 6.2. Implications for Scientific Understanding

With the limited representation of ecological feedbacks, current ESMs have little capacity to assess the potential for ecological change, tipping points, and state transitions in response to anthropogenic change (Armstrong McKay et al., 2021; Hense et al., 2017; Verburg et al., 2016; Moore, 2022; Appendix A). As previously noted, some ecological feedbacks are included in large-scale models, albeit often highly simplified due to computation constraints and/or knowledge/observational gaps. However, research is often carried out within ecosystem compartments (e.g., plants, animals, or microbes), ignoring important interactions throughout whole food webs, and across scales (Bonan et al., 2024; Burkepile & Thurber, 2019; Ransome et al., 2023; Williams et al., 2024). Models that capture aspects of ecological interactions in ecosystems and with physical and biogeochemical processes exist, but these have generally not been incorporated into current ESMs (see Appendix A). In part, this is due to many ecological processes occurring at finer scales than current ESMs resolve, yet aggregated changes are likely to have important regional and potentially global consequences (Bonan & Doney, 2018). For those processes that are incorporated in ESMs, improvements are required to fully capture the ecological feedbacks (Bonan & Doney, 2018; Fisher & Koven, 2020; Hense et al., 2017; Liu et al., 2019; Wan & Crowther, 2022; Appendix A).

To determine the importance of ecological feedbacks in the Earth system, we need to understand how ecological interactions generate feedbacks across ecosystems over scales of thousands of kilometers, across continents and oceans, and over decades to centuries. Current approaches to scaling-up across ecosystems to larger spatial scales generally involve biome categorization and biogeographic analyses with broadly defined boundaries between ecosystem types (e.g., Costello et al., 2017; Longhurst et al., 1991). However, many ecological processes operate over a broad range of spatial and temporal scales (Gonzalez et al., 2020; Levin, 1992; Murphy et al., 1988; Schneider, 2001; Steele, 1978), which, as we have noted, can subsequently lead to cross-scale ecological feedbacks (Gonzalez et al., 2020; Pichon et al., 2024; Stoy et al., 2009; Thompson et al., 2021; Figure 4). A wide range of different model approaches are being developed that provide a promising basis for exploring the temporal development of ecological feedbacks across scales. For example, terrestrial vegetation demographic models are able to simulate size and age structure of patches within forests, while gap models simulate individual tree responses to explore the development of multispecies assemblages and long-term dynamics of forest ecosystems

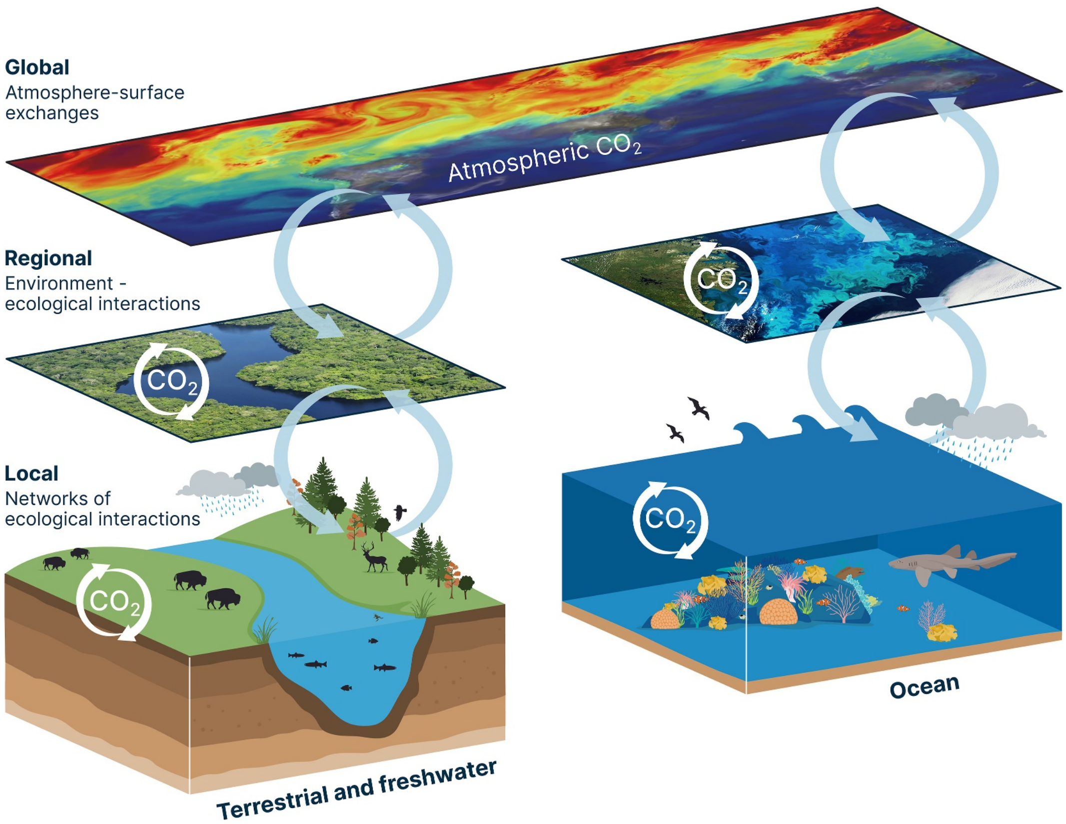


**Figure 4.** Ecological feedbacks at multiple scales: an example focusing on $CO_2$ pathways. Global carbon fluxes and storage processes across ecosystems are a function of ecological processes and feedbacks involving atmosphere-surface interactions, environment-ecological interactions, and biotic interactions operating at regional (hundreds to thousands of kilometers) and local (<100 km) scales (Fulton et al., 2019; Liang et al., 2022; Miller & Allesina, 2023; Talbot et al., 2022; Ware et al., 2019). Non-$CO_2$ pathways will also influence these processes (not shown; see Bonan et al., 2024). Ecological processes operate over a wide range of spatial and temporal scales as a result of organism behaviors, life cycles, trophic interactions, organism-environment interactions, evolutionary processes, and ecosystem—land, -ocean, and -atmosphere interactions. There is often a mismatch between the scales over which the major physical and chemical processes operate (including how they are represented in models) and the scale of operation of many ecological processes. The result is that many ecological feedback cycles are missing from current models (Fulton et al., 2019; Jackson & Fahrig, 2015; Moore, 2022; Trappe & Chisholm, 2023; Wan & Crowther, 2022).

(Fischer et al., 2016; Shugart et al., 2020). For the ocean, model development of ecological processes for incorporation in ESMs is addressing aspects of biogeochemical pumps (e.g., Armstrong McKay et al., 2021), trace gas, and biogeophysical processes (see Appendix A). Regional models are being developed to examine processes in particular areas, for example, a coupled atmosphere-ocean-biogeochemical model developed for the Great Barrier Reef region is being used to examine the role of the coral reef in the generation of marine DMS and regional atmospheric processes (Jackson et al., 2022). Despite these and other extensive modeling efforts being developed to improve understanding of the role of ecological processes in the Earth system, they remain largely peripheral to mainstream ESM modeling efforts (Bonan et al., 2024; Kyker-Snowman et al., 2022). Current predictions about the future of the Earth system are often based on implicit assumptions about the operation of ecosystems over large temporal and spatial scales, which, given the limited understanding, requires caution in interpretation and presentation of model results. Understanding feedbacks occurring over decadal scales is critical for informing decision making for conservation and management, but presents major challenges for modeling and prediction (Bonan & Doney, 2018; Melbourne-Thomas et al., 2023; Muller et al., 2021; Payne et al., 2022).

Generating highly complex models that link physical, chemical, and biological systems involves major issues around uncertainty, particularly those associated with the underlying processes, system structure, interactions between processes and model parameterization (Fulton et al., 2019; Verburg et al., 2016). Incorporating ecological feedbacks adds further difficulties, which are exacerbated when societal/human interactions are included (Verburg et al., 2016) (Appendix A). Models are required that include ecological feedbacks without generating unrealistically complex coupled model systems that are unlikely to yield useful insights and results. Despite the challenges, strategies and practical modeling approaches are being developed that emphasize the importance of alternative pathways and model structures to represent ecological processes, and are starting to include cross-scale interactions and societal-ecological interactions (e.g., Fisher & Koven, 2020; Fulton et al., 2019; Hamann et al., 2018; Thompson et al., 2021; Wan & Crowther, 2022). For example, integrated modeling of socio-ecological systems in the Bering Sea ecosystem downscales physical and biogeochemical projections derived from ESMs under different scenarios, to project future marine ecosystem structure and functioning using a range of ecosystem models of varying complexity (Hollowed et al., 2020). Further, the Fisheries Ecosystem Model Intercomparison Project (FISHMIP) network uses an ensemble approach based on multiple ecosystem models to explore the impacts of climate change and fisheries in marine ecosystems at global and regional scales (Tittensor et al., 2021). Modeling approaches have also been developed that explicitly include a range ecological feedbacks, and in which community structure and diversity evolve as emergent properties (e.g., the Darwin model; Dutkiewicz et al., 2020; Follows et al., 2007; Krinos et al., 2025).

These proposed strategies for model development highlight the need to improve the representation of ecological and socio-ecological processes in ESMs, the importance of increased modeling capacity (expertise and computational), the need for improved dialog and joint collaborative activities between ecologists and modellers from different disciplines, and a more inclusive approach to encompass different perspectives of the natural world (Bonan et al., 2024; Kyker-Snowman et al., 2022; Melbourne-Thomas et al., 2017; Weiskopf et al., 2022).

Scientific advances are providing novel ways to explore ecological feedbacks. For example, innovations in artificial intelligence/machine learning are transforming our capacity to analyze large multivariate data sets and develop of new modeling approaches that can encompass a wider range of ecological processes and reduce computational demands (Ban et al., 2022; Butt et al., 2023; Curasi et al., 2022; Sun et al., 2023). Ecological network analysis has also proven to be a useful tool for exploring feedbacks. Despite often being based on highly simplified perspectives, there are valuable studies of ecological networks that are based on biotic and abiotic-biotic interactions in ecosystems, which allow exploration of potential feedbacks using appropriate network metrics (e.g., Ward et al., 2022). These need to be extended to include spatial and temporal variability and approaches are being developed that allow analyses of more complex network structures (e.g., including spatial structure and multilayer networks; Fulton et al., 2019; Muller-Hansen et al., 2017; Nogues et al., 2022).

The discussion above demonstrates that evaluating the role of ecological feedbacks in the Earth system requires more than a simple two-way perspective of individual interactions. To fully understand how ecosystems operate and influence the Earth system, it is essential to account for the complexity of interconnected interactions—both within and between ecosystems—including multiple, often uncertain feedbacks.

### 6.3. Policy Implications

As with all types of policy, there are trade-offs to be made. In the case of environmental policy, these trade-offs attempt to balance human requirements with a biologically diverse and healthy planet. For example, should a forest be fully protected from human use for its rich diversity and endemic species, or allow some sustainable exploitation to provide a service to humans?

Conserving ecosystems and their functioning within the Earth system requires environmental policy, and the policy decision-making process needs to account for the spatial and temporal scale of the ecological feedbacks discussed here. For instance, the timescale of the environmental policy needs to cover the different temporal processes occurring within the forest, which may be occurring over a longer timeframe than the policy allows. Spatially, ecological feedbacks do not adhere to national boundaries, thus requiring cooperation between neighboring countries or other jurisdictions to produce suitable environmental policies. For example, for an environmental policy focused on a forest, the ecological feedbacks may involve processes at the local (forest) spatial scale that impact processes at the regional or global scale. The required cooperation is already occurring in some cases. For example, trans-jurisdictional cooperation is required for management and policy making in the Southern Ocean, where ecosystems are protected within international waters. With the acceptance of the biodiversity beyond national jurisdiction (BBNJ) treaty on the High Seas (United Nations, 2023), there is scope to manage open-ocean waters for the first time.

For environmental policies to be effective, they need to be adaptable to environmental changes. The development of adaptive Ecosystem-Based Fisheries Management (EBFM) fishery policies provides some useful context (Holsman et al., 2020). Although there remain challenges in incorporating climate change, the EBFM approach can provide multiple benefits, including sustaining the protein and micronutrient supply for human use, ensuring future fish populations that can be exploited sustainably, and allowing the natural food webs to be maintained to a level that avoids total ecosystem or food web collapse. However, these fishery policies do not yet cast a wider net to look holistically at the impact of fishing on the Earth system. For instance, impacts just starting to be considered include the carbon released by bottom trawling that has been stored in the seabed for decades to centuries, with the aim in the future to expand analyses to consider potential trophic cascades (shifts in food webs), which may alter the functioning of the biological carbon pump and storage systems (Cavan & Hill, 2022; Epstein et al., 2022). On a positive note, research into these fishery-carbon feedbacks and talks between policy makers and scientists are starting to happen (ICES, 2024), providing a useful case study to stimulate parallel work relevant to other environmental policies in different terrains.

## 7. Priorities

Our synthesis of available information and current understanding of ecological feedbacks supports the view that these feedbacks play a crucial role in a wide range of Earth system processes at local, regional, and global scales. Many ecological processes underpinning feedbacks in ecosystems across the world have already been disrupted, with further major changes expected over the next few decades, the consequences of which are largely unknown. Key policy decisions for mitigating and adapting to the projected changes will require scientific advice that explicitly considers ecological feedbacks and their potential to generate impacts that current Earth system projections may miss.

Incorporating ecological feedbacks and the interconnected functioning of ecosystems across multiple spatial and temporal scales provides a foundation for developing ESMs and for projecting the magnitude, direction, and broader consequences of future changes in the Earth system. Accounting for these feedbacks in assessments of anthropogenic impacts on ecological systems is critical for generating projections of future social-ecological interactions and feedbacks, ensuring the scientific advice underpinning policy development is both realistic and relevant. We identify three priority areas for future research:

1. Including ecological feedbacks in assessments of global change and ESMs

Identifying and quantifying the knowledge gaps surrounding the mechanisms involved in how ecological processes influence biophysical and biogeochemical processes in different ecosystems across the world and in the development and resilience of ecosystems is a high research priority. Central to this challenge is clarifying why particular ecological feedbacks matter, what processes (e.g., ecosystem structure and functioning, biophysical or biogeochemical), ecosystem services (e.g., food, water, climate regulation, nutrient cycling, flood control) and Earth system processes (e.g., carbon and methane budgets, surface -atmosphere radiation budgets) are affected, and over what spatial and temporal scales. Research focused on evaluating the interactive effects of ecological feedbacks in response to multiple drivers of change is a particular need. Models that explicitly consider ecological feedback mechanisms within ecosystems, including pathways involving physical and biogeochemical processes, to examine how they influence responses to change, and ecosystem outcomes (abiotic and biotic) are critical and remain to be developed. Potential foci include developing metrics to quantify the sign, strength, and scale of ecological feedbacks following multiple changes in ecosystems, and under different conservation and management objectives (e.g., Xiao et al., 2019). Furthermore, leveraging alternative modeling approaches and rapid advances in observational capacity is required to address a series of fundamental issues, including, (a) determining responses and transient dynamics of ecosystems to multiple changes (abiotic and biotic) and how are these modified by ecosystem degradation, (b) predicting major features of ecosystems and emergent properties, including structure, functioning, and traits of key species, and (c) developing coupled ocean-land-atmosphere-biosphere models.

2. Incorporation of ecological feedbacks across scales

To overcome the limited understanding of the combined impacts of climate change and biodiversity loss across large regions, emphasis should be directed at developing research initiatives designed to evaluate the integrated operation of ecosystems, between ecosystems, across scales, and their influence in global-scale processes. This includes (a) how ecological processes influence biophysical and biogeochemical processes in different ecosystems and across scales, (b) the operation of ecological feedbacks in response to variability (and changing frequencies of variability), and (c) responses to variability through time lags in feedbacks within and between ecosystems. Suggested foci for these research initiatives are the emergence of structure (e.g., a particular food web, a forest or coral reef) at different scales, the processes involved, and how the new structures generate further interactions, such as: life cycles of species with large scale (>100 km) population distributions that operate in large ecosystems or between multiple ecosystems, processes connecting ecosystems across scales (e.g., patterns of seasonal migration and food web connections), and magnitudes of movements of nutrients, energy and organisms and ecological interactions in boundary regions between ecosystems. Quantitative understanding is also needed to assess the potential for ecological feedbacks to generate surprises in Earth system processes in response to climate change and biodiversity loss, including the diverse mechanisms involved in tipping points (Brook et al., 2013; Kopp et al., 2025) and cascading effects, and whether combined local changes may result in regional or global impacts.

3. Suitable projections for policy advice

Policies intended to promote conservation and sustainable management require information and projections of the effects of change on ecological systems on time scales of years to decades and to centuries (Beckage et al., 2020; Bonan & Doney, 2018). The rapid changes that have occurred over the last few years in the Earth system (Fretwell et al., 2023; Hong et al., 2023; Perkins-Kirkpatrick et al., 2024; Schoen et al., 2024) have highlighted the urgent need for information at multiple time scales (Earth system prediction; Bonan & Doney, 2018; Payne et al., 2022). Policy makers will increasingly need science-based advice on shorter time scales to determine solutions that address the economic, industrial, and societal implications of changes affecting ecological feedbacks already underway. Policy development also requires quantitative understanding of socio-ecological feedbacks, and the global implications of activities and decisions made at local and regional scales that affect ecological systems and feedbacks. Specific and relevant models and projections are required that allow the flexible assessment of multiple risks, model forecast skill (Kempf et al., 2023) and alternative policy scenarios. Development of standardized and open model interfaces to ESMs model data that generate downscaled projections (Drenkard et al., 2021; Hermann et al., 2021) can provide the basis for generating the relevant projections required for specific local areas (hundreds to thousands of kilometers).

The above priorities highlight that there are extensive modeling initiatives on which a focus on ecological feedbacks can be developed, but it is crucial that study extends beyond individual feedbacks. Within ecosystems, there are multiple simultaneous pathways of influence, while socio-ecological interactions add further feedbacks. The current pathway of ESM development is not aimed at improving the representation of fundamental processes determining ecosystem structure and functioning and associated feedbacks. Generalized ecosystem models for ocean, land, or global application for projecting the major impacts of future environmental change are important in providing information. However, in addition to general ecosystem models, models are required that provide enhanced resolution of the ecological structure and functioning in different ecosystems and include the capacity to develop in response to change. Rapid developments in data collection and observational capacity (e.g., satellite and autonomous systems) and in the use of AI/machine learning in conjunction with dynamic models provide an opportunity to develop the new generation of models required. To generate fully operational ESMs, we suggest that a new parallel but collaborative international effort with the ESM community is required, with an integrated interdisciplinary focus that explicitly explores ecological feedbacks across scales (spatial and temporal), and the development of global ecosystem models.

## 8. Next Steps

Facilitating research needed to address the above priority research areas requires development of a systematic scale-based approach designed from the outset to improve quantitative understanding of ecological-environment interactions and feedback processes at different scales. This will involve:

1. Focused field studies designed to develop quantitative understanding and analyses of specific feedback processes for a range of terrestrial and ocean ecosystems at different scales,
2. Targeted sustained monitoring and observation programmes, including new technologies and analyses, to provide detailed characterizations of key processes at different scales (e.g., connectedness between ecosystems, including animal movement and migration),

3. Improve representation of ecological feedbacks in ESMs at a range of scales, to improve our capacity to assess for potential ecological changes, the likelihood of tipping points and changes in state through anthropogenic changes,
4. Interdisciplinary modeling efforts that merge alternative perspectives and multiscale approaches (including downscaling and regional modeling) with a specific focus on ecological feedbacks and cross-scale connections,
5. Co-development of risk-based approaches associated with ecological feedbacks in ecosystems for decision making for conservation and management and policy development,
6. A complimentary parallel effort to that of the ESM community aimed at the generation of whole ecosystem models that can be applied at multiple scales, and as a coupled component in Earth system simulations.

Researchers have long argued the value of greater integration between the terrestrial, freshwater, and marine ecological scientific communities (Fulton et al., 2019; Steele, 1985). A central focus on ecological feedbacks across scales in the Earth system could provide the basis for developing a more integrated approach based on shared understanding and expertise within the ecological scientific community. In addition, multi-disciplinary approaches and importantly, approaches informed by diverse human perspectives (Appendix B) allow the complex interactions involved in Earth's ecological feedback mechanisms to be understood and quantified (Bonan & Doney, 2018; Gonzalez et al., 2020). Our ability to obtain, transfer, and share data (at comparatively low costs), is unprecedented and already fully integrated in modern society (e.g., social media), and our analytical capability is on the cusp of being transformed by the development of AI/machine learning tools (Ban et al., 2022; Butt et al., 2023). These current and emerging capabilities must be capitalized to ensure that fundamental understanding is achieved before time runs out to gather data needed to address the ecological, social, and policy issues associated with rapid climate change. Monitoring, understanding, and working toward maintaining and sustaining the operation of critical ecological feedbacks will ultimately ensure a higher percentage of people have access to life's essentials.

## 9. Conclusions

Ecological feedbacks are a fundamental aspect of the Earth system, and are being disrupted by the combined impacts of ecosystem degradation and climate change, resulting in greatly increased societal risks. Our review highlights the critical need for the development, quantification, and integration of ecological feedbacks within Earth system analyses, not only to enhance our understanding, but also to provide critical science-based advice to inform policy development and decision-making. The approach proposed herein, of a systematic scale-based approach to the analyses of ecological feedbacks, supports the requirement for understanding their role within and between ecosystems at a variety of temporal and spatial scales. That in turn supports the need for integrated analyses of combined process, observations, and modeling studies that can yield policy-relevant advice. This scale-based approach can be applied to underpin combined analyses of terrestrial, freshwater, and marine ecological systems and provides a framework to bring together complementary perspectives, knowledge, and expertise. The increasing need for science-based advice to support solutions to address the economic, industrial, and societal impacts of changes that are already underway, and expected to accelerate, places an ever-increasing urgency on integration of ecological feedbacks into our understanding of Earth system processes.

## Appendix A: Current Status of Representation of Ecological Processes and Feedbacks in Earth System Models

Earth System Models (ESMs) have been developed to improve our understanding of the factors affecting global climate and biogeochemical cycles and predict a future Earth under climate change scenarios (Bonan & Doney, 2018; Friedlingstein, 2015; Friedlingstein et al., 2006; Jones, 2020). They simulate physical, chemical, and biological processes that determine the future status of the land, ocean, cryosphere and atmosphere of the Earth. The current generation of ESMs are largely focused on the physical and biogeochemical processes influencing climate, and the inclusion of biological processes remain relatively limited (Bonan & Doney, 2018). The development of ESMs has been a major focus of modeling efforts coordinated through the IPCC (Intergovernmental Panel on Climate Change) Coupled Model Intercomparison Project (CMIP; Eyring et al., 2016), which is now in its seventh phase (CMIP7). This appendix gives a brief overview of the ecological processes and feedbacks that are currently accounted for within ESMs, and highlights some key ecological processes that need to be explored and incorporated to enhance our understanding of ecological feedbacks.

### A1. ESMs: Ecological Feedbacks in the Marine Biosphere

Of approximately 100 climate models used in CMIP6 and the last IPCC report (IPCC AR6, 2022 ; IPCC, 2022), 28 include a representation of marine biogeochemistry, and as such, a representation of marine ecosystems. The representation of ecosystems in these models is highly idealized with 1 or more phytoplankton functional types (PFTs) and 1 or more zooplankton functional groups (Kearney et al., 2021; Planchat et al., 2023; Séférian et al., 2020). Marine ecological processes involved in feedbacks influencing climate within ESMs can be subdivided into those that affect i, biogeochemical pumps, ii, biologically-derived trace gases, and iii, biogeophysical mechanisms (Hense et al., 2013).

#### A1.1. Biogeochemical Pumps

ESMs that include a marine biogeochemical component represent the growth and/or biomass of primary producers (e.g., phytoplankton) constrained by temperature (Eppley, 1972), light and nutrient availability (Laufkötter et al., 2015), and zooplankton grazing (Rohr et al., 2023). These ESMs isimulate at least one phytoplankton macronutrient (e.g., nitrate or phosphate), with many also representing micronutrients such as iron (a determinant of high nutrient low chlorophyll regions) and silicate (a critical nutrient for diatoms). Pelagic calcification, an important determinant of ocean alkalinity and therefore air-sea carbon fluxes, is simulated implicitly in CMIP6 ESMs without a calcifying PFT (Planchat et al., 2023). ESMs generally show a reduction in biologically derived carbon export production in response to climate change but with a high divergence in the magnitude of this decline (Henson et al., 2022). This coincides with a slowdown in the overturning circulation that reduces anthropogenic carbon uptake by the physical pump yet enhances deep-ocean carbon storage by the biological carbon pump (Liu et al., 2023; Wilson et al., 2022).

#### A1.2. Biologically Derived Trace Gases

In addition to air-sea carbon fluxes, marine biota also influences the air-sea fluxes of other climate forcing agents such as dimethylsulfide (DMS; Charlson et al., 1987) and $N_2O$ (Martinez-Rey et al., 2015). Within CMIP6, only 5 ESMs simulated the ocean fluxes and climate feedbacks of ocean DMS with that decreasing to 4 ESMs for $N_2O$ (Séférian et al., 2020). There is no consensus among the different models, on even the sign of change of DMS emissions with anthropogenic climate change (Bock et al., 2021), in part because its parameterization is dependent on ocean productivity, which is itself very poorly constrained in recent ESM ensembles (Kwiatkowski et al., 2020; Tagliabue et al., 2021). To date, a very limited number of studies have been published so it is difficult to assess the significance of ocean $N_2O$ climate feedback loops (e.g., Buitenhuis et al., 2018; Martinez-Rey et al., 2015).

#### A1.3. Biogeophysics

Marine biota may also influence ocean physics and hence the physical climate through changes in ocean surface albedo, water column light attenuation, or turbulent viscosity changes. The inclusion of feedbacks between phytoplankton concentration and upper ocean heat penetration is represented in some ESMs (e.g., IPSL-CM6A; Boucher et al., 2020). The climate impact of light absorption by phytoplankton has been assessed in several ESMs and shows significant effects on oceanic and atmospheric temperature, sea-ice cover (Asselot et al., 2022; Lengaigne & Vecchi, 2010; Patara et al., 2012) and El Niño-Southern Oscillation (ENSO) dynamics (Jochum et al., 2010). The effect on climate through biologically induced changes in the ocean's turbulent viscosity has not yet been addressed, although idealized studies show potentially large effects at regional scales.

#### A1.4. Uncertain and Missing Ecological Processes

Poorly constrained or missing ecological processes with known climate feedbacks in ESMs include the simulation of diazotrophy (Bopp et al., 2022), phytoplankton stoichiometry (Kwiatkowski et al., 2018), microbial respiration (Henson et al., 2022), vertical migration (Siegel et al., 2023), the thermal sensitivity of ecological processes (e.g., Taucher & Oschlies, 2011), planktonic sensitivities to ocean acidification (Planchat et al., 2024; Tagliabue et al., 2011), particle characteristics (Henson et al., 2022), and zooplankton grazing (Rohr et al., 2023).

In addition, a number of ecological processes that can influence projections of climate feedbacks have been represented in ocean-only models, but not yet incorporated in ESMs (typically because of the associated computational cost). This includes the simulation of explicit pelagic calcifiers such as coccolithophores (Krumhardt et al., 2019), foraminifera and pteropods (Buitenhuis et al., 2019), interactions with higher trophic levels (Dupont et al., 2023; Tittensor et al., 2021) and anthropogenic drivers such as fisheries (Pershing et al., 2010) and microplastics (Richon et al., 2022).

Benthic ecosystems including coral reefs are currently unresolved by ESMs despite acting as non-negligible sources of atmospheric $CO_2$ (Frankignoulle & Canon, 1994) and being highly susceptible to climate change (Cornwall et al., 2021). Similarly, coastal blue carbon ecosystems such as seagrasses, mangroves and salt marshes are also currently unresolved, despite their role in the carbon cycle (Duarte et al., 2005; Filbee-Dexter et al., 2024).

### A2. ESMs: Ecological Feedbacks in the Terrestrial Biosphere

The latest generation of ESMs include a range of ecological feedbacks that encompass biogeophysical and biogeochemical interactions between the terrestrial biosphere and the physical environment. Many of these feedbacks involve vegetation and fundamental microbial processes, whereas the consideration of animals is generally limited.

#### A2.1. Ecological Feedbacks Involving Vegetation

Vegetation plays a crucial role in the balance of radiation, energy, water, carbon, and nutrients in the Earth system, and is represented to some degree in almost all ESMs in the CMIP6 model comparison project. Yet, only a few ESMs include Dynamic Global Vegetation Models (DGVMs), for example, DYNVEG in MPI/JSBACH (Reick et al., 2013) and TRIFFID UKESM/JULES (Cox, 2001). The key challenges of DGVMs lie in scaling processes from individual trees to >100 km scale, and in balancing complexity with increasing uncertainty and computational feasibility (Argles et al., 2022). Therefore, vegetation is represented in most ESMs by leaf area, stomata on leaves, and carbon and nitrogen pools (Bonan, 2016). Vegetation distribution is represented mostly as cohorts or a fractional coverage of plant functional types, a concept that is increasingly criticized for its oversimplification of vegetation dynamics (Argles et al., 2022; Page et al., 2024).

Most land surface models have established vegetation-atmosphere feedbacks related to the surface albedo and its effects on the radiation balance. For example, positive vegetation-snow-masking feedbacks are a key accelerator of warming in boreal regions (e.g., Abe et al., 2017; Brovkin et al., 2013; Thackeray et al., 2014). Equally important, both positive and negative evapotranspiration feedbacks have been extensively studied with ESMs, for instance in the Sahel region (Claussen & Gayler, 1997; Rachmayani et al., 2015) and in the context of the Amazon dieback (Betts et al., 2004; Boulton et al., 2013). While these large-scale processes are relatively well represented, challenges remain in capturing the spatial heterogeneity and fine-scale interactions that govern the turbulent exchange of heat, momentum, water, and trace gases—particularly the effects of vegetation structure and surface roughness (Bonan & Doney, 2018; de Vrese et al., 2016). The role of plant diversity adds another layer of complexity, influencing these fluxes and feedbacks in ways that are not yet fully resolved in current ESMs and could benefit from stronger links with ecological research (Claussen et al., 2013; Groner et al., 2018; Pavlick et al., 2013).

Physical and biogeochemical $CO_2$-stomata-feedbacks are a fundamental component in many ESM's carbon and water cycle (Heinze et al., 2019). These processes were initially added to ESMs because of the potential for large climate feedbacks arising from the carbon cycle (Bonan & Doney, 2018), for example, in CMIP climate sensitivity experiments (Meehl et al., 2020). Most ESMs consider some sort of optimization between carbon uptake by the land (photosynthesis) and water loss from it (transpiration and leaf evaporation), which depends on soil moisture and boundary layer atmospheric humidity. Some models account for the allocation of assimilated carbon into different plant parts that impacts plant growth, biomass accumulation, changes in terrestrial carbon storage, and feedbacks on atmospheric $CO_2$ and climate (Bonan & Doney, 2018; Fisher & Koven, 2020; Heinze et al., 2019).

Most land surface models simulate the timing of biological events (phenology), such as flowering and leaf shedding, influenced by seasonal and climatic variations, which affect ecosystem productivity and (often implicitly) competition for resources like light and water (Argles et al., 2022; Bonan et al., 2024). DGVMs additionally simulate the dynamics of vegetation over time, including the establishment, competition, and mortality of different plant functional types or cohorts of individual trees. These dynamics can change vegetation cover and composition in response to climatic conditions and disturbances such as wildfires (Harris et al., 2016). Fire feedbacks are a key component of many ESMs, however the representation varies from simple disturbance factors (e.g., DYNVEG) to advanced fire schemes (e.g., SPITFIRE).

### A2.2. Ecological Feedbacks Involving Terrestrial Microbes

Microbes play an important role in decomposing organic matter, cycling nutrients, and influencing soil and atmospheric chemistry, all of which are fundamental to the dynamics of Earth's climate systems. Although microbial processes are integral to many ESMs, the level of complexity in representing microbial dynamics can vary significantly among different models. This variability reflects both the microscale nature of microbial processes and the immense diversity of microbial functions, which remain difficult to observe and quantify globally. Among the latest generation of models contributing to CMIP6 (Eyring et al., 2016), 23 included an interactive carbon cycle and 15 incorporated the coupled nitrogen cycle (Gier et al., 2024) and associated feedbacks.

Many ESMs simulate the decomposition of organic material through their land surface component (e.g., CESM2/CLM5, MPI-ESM1-2/JSBACH3.2, UKESM1/JULES-ES-1.0 in CMIP6), as decomposition is integral to the carbon cycle. Microbial processes such as methanogens and methanotrophy are critical for modeling methane emissions and associated feedbacks, particularly from wetlands, rice paddies, and other anaerobic environments; these are included for example, in CanESM5/CTEM1.2 and UKESM1/JULES-ES-1.0 (Parker et al., 2022). Many models also represent nitrification and denitrification, to account for effects of nitrogen availability on plant growth and feedbacks associated with greenhouse gas emissions (e.g., CESM2/CLM5, ACCESS-ESM1-5/CABLE2.4; Thomas et al., 2015; Lawrence et al., 2019). In addition, a few models consider the symbiotic relationships between plant roots and mycorrhizal fungi, which can enhance plant nutrient uptake (especially phosphorus) in exchange for carbohydrates (e.g., GFDL-ESM4/LM4.1; Sulman et al., 2019). This interaction can feedback on climate via plant growth, soil carbon storage, and nutrient cycling.

### A2.3. Ecological Feedbacks Involving Terrestrial Animals

Although animals play a significant role in biogeochemical cycles, vegetation dynamics, and other processes in the Earth system, the representation of animals in ESMs is still relatively simplistic and not as dynamically integrated as plant and microbial processes. This is partly due to the history of model development, and partly due to the complexity of animal behaviors and the vast diversity of animal roles in ecosystems, which are challenging to quantify and model accurately, and would require enormous computational resources.

Nevertheless, some ESMs are beginning to incorporate some ecological feedbacks that include animals (Bonan & Doney, 2018), particularly those focusing on agricultural impacts on climate. For example, specific versions of LPJ-GUESS (Pachzelt et al., 2013) and DLEM 3.0 (Dangal et al., 2017) include a grazing scheme to account for mammalian herbivore population responses to different environments and their impacts on biogeochemical cycles. Others have implemented a manure scheme to investigate the magnitude, temporal variability and spatial heterogeneity of nitrogen pathways on a global scale, for example, in CESM (Hess, 2021; Riddick et al., 2016).

## Appendix B: Social-Ecological Feedbacks in the Earth System

Social-ecological systems are complex adaptive systems (Preiser et al., 2018), with changes in one part of the system potentially causing disproportionate and unpredictable changes in other parts, which in turn influences additional parts of the system. Social-ecological feedbacks can occur at a variety of spatial scales—local, regional, and global—and on different timescales, from sub-decadal to many thousands of years (Chaffin & Scown, 2018; Donges et al., 2021; Lafuite & Loreau, 2017). Indeed, many of the feedbacks described in the main text could be considered as social-ecological feedbacks because ecological feedbacks are influenced by human activity, and society is in turn affected by changing access to ecosystem services. The acknowledgment that human activities have a global impact on Earth system processes has emphasized that management of those activities (e.g., ozone and greenhouse gas emissions or microplastic pollution) is required for a sustainable future for humanity. Many human activities affecting ecosystems are, however, considered piecemeal at local or national scales (e.g., deforestation, changing land-use or fisheries), with little consideration of the combined impact of such activities, or the potential for generating social-ecological feedbacks and negative outcomes at regional and global scales.

An example of a large-scale social-ecological feedback (continental scale and occurring over millennia) is the way in which Aboriginal fire management has shaped ecological communities in Australia (Bliege Bird et al., 2018; Bowman, 2003; Bowman et al., 2011). There is increasing evidence that sustained Aboriginal fire use over tens of thousands of years shaped many Australian landscapes by sharpening vegetation boundaries, maintaining open vegetation, and creating habitat for game species. Skilled burning reduced the extent and intensity of fires, allowing fire-sensitive plant communities to persist in flammable landscapes (Bowman, 2003). Disruption of Aboriginal fire regimes through European colonization, together with the impacts of anthropogenic climate change, has led to increased fuel loads and large-scale, high intensity bushfires (Bowman, 2003). Adapting the principles of Aboriginal patch burning and enabling Indigenous-led fire management can be important in strategies for improvement of fire management and biodiversity outcomes across Australia (Smith, Neale, & Weir, 2021).

At smaller spatial and temporal scales, social-ecological feedbacks in agrifood and natural resource harvesting systems can lead to so-called "wicked resilience" (Glaser et al., 2018)—also referred to as "social-ecological traps" (Cinner, 2011)—where interlocking cycles in social-ecological systems can drive negative outcomes for people and for ecosystems. Glaser et al. (2018) give an example of the Spermonde Coral Reef Archipeligo, where increasingly intensive fishing operations are driven by local social factors, leading to loss of large fish, damage to reef habitats the spread of algae, which combined with other anthropogenic impacts, leads to further reef damage. These impacts change the habitats and reef community structure, which in turn leads to further intensification of fishing effort. The authors argue that breaking such feedbacks at multiple levels is needed to move toward sustainable human-nature relations from the local to the global level (Glaser et al., 2018).

Social-ecological feedbacks have occurred over millennial timescales, as humans and ecological systems have coevolved. The feedbacks between people and nature shape culture—stories, customs and beliefs (e.g., Roberts et al., 2021). In some cultures, the narratives might be around control of nature (and the threats it contains), while in others the narratives are about caring for nature. Those narratives then affect emergent cultural attitudes to ecosystems; as a threat that needs to be tamed, a resource to use, or as systems to be nurtured (such that maintaining ecosystem health is synonymous with maintaining human health, e.g., see Fischer et al., 2022).

Bringing an explicitly social-ecological lens to the consideration of feedbacks in the Earth system can provide opportunities to co-design solutions to undesirable feedbacks by including perspectives and needs of diverse communities, or to enhance feedbacks that support sustainability transitions. Potential opportunities to enhance the understanding of ecological feedbacks in the Earth system through knowledge weaving from Indigenous Ecological Knowledge exist (Woodward et al., 2020). Many Indigenous cultures describe time as having a "circular" or "cyclic" form (Janca & Bullen, 2003), which is arguably more aligned with understanding ecological feedbacks than the Judeo-Christian linear concept of time (see also Melbourne-Thomas et al., 2023), as is the understanding in many Indigenous cultures of humans as part of nature rather than separate to it.

## Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

## Data Availability Statement

Data were not used, nor created for this research.

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